EURASIAN WEED INFESTATION IN WESTERN MONTANA IN RELATION TO VEGETATION AND DISTURBANCE

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Abstract

Along a vegetational gradient from cool-moist subalpine forests to warm-dry steppe, Eurasian weed infestation was restricted to the low-montane (*Pinus ponderosa*) to dry steppe (*Bouteloua/Stipa*) portion of the gradient for relatively undisturbed vegetation. With intensive disturbance the infestation segment of the gradient was extended through the mid-montane (*Pseudotsuga menziesii*) zone. The subalpine (*Abies lasiocarpa*) zone was essentially weed-free with or without disturbance. In the absence of deep shade, weed infestation was correlated with mean July temperature.

During a survey of exotic weeds in Montana in August 1980, we observed that roadside weeds can invade adjacent native vegetation in significant numbers, but only within a restricted segment of a vegetation gradient (i.e., temperature-precipitation). Moreover, if the native vegetation is disturbed, the range of infestation along the gradient is extended. In this report we document these observations along a transect from cool-moist subalpine forests to warm-dry grasslands in western Montana. Additionally, we explore a few of many possible reasons for such differential weed infestation.

Methods

Along US Highway 12 from Lolo Pass (1700 m; $46^{\circ}38'N$, $114^{\circ}36'W$) to the Waterworks Hills just northeast of Missoula, Montana (1040 m; $46^{\circ}53'N$, $113^{\circ}59'W$) 14 paired roadside/native vegetation plots were surveyed. Plots were 5 m by 50 m (narrower if roadside communities were less than 5 m wide) with the long axis positioned parallel to the roadside. Native vegetation plots were always 5 m distant from the roadside/native vegetation boundary. This distance assured the possibility of weed diaspore dispersal into our plots, but was far enough from the road edge to preclude previous and/or continuous physical disturbance. A vascular plant species list, as complete as possible, was recorded in each plot along with species-specific cover-abundance data (sensu Braun-Blanquet 1964). The habitat type (~plant association) of each native vegetation plot was identified through the dichotomous

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vegetation keys provided by Pfister et al. (1977) for forests, and Mueggler and Stewart (1980) for grasslands.

Eighteen forest vegetation plots that had been clearcut 1–7 years prior to sampling were surveyed as described above. These plots spanned the mid- to high-montane vegetation zones of the region. Habitat types of clearcut plots were identified by inspection of neighboring undisturbed forests of similar slope and aspect when possible, otherwise from the presence or absence of indicator species in the plots themselves. (In no cases were Eurasian weeds found in neighboring undisturbed forests.) Clearcut plots were located in Flathead, Granite, Lincoln, Mineral, and Missoula Counties, Montana.

Indices of similarity (Bray and Curtis 1957) between roadside plots and native vegetation were calculated using (1) species presence, and (2) species coverage. Percent coverage (Daubenmire 1959) was calculated by converting Braun-Blanquet cover-abundance scale data to the appropriate average percent, i.e., 5 = 88%, 4 = 63, 3 = 38, 2 =15, 1 = 3, $\pm = 0.5$, and r = 0.1.

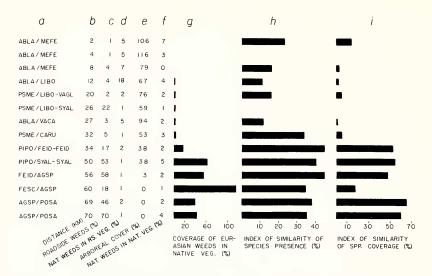
Weed species were divided into two categories for the purpose of this report. (A) the first category was introduced Eurasian taxa that are generally considered to be troublesome to human endeavors (Reed 1971, and see lengthy discussions of "weed" in Baker and Stebbins 1965). This category included taxa such as Bromus japonicus, B. tectorum, Centaurea maculosa, Cirsium arvense, C. vulgare, Filago arvensis, Lactuca serriola, Melilotus alba, M. officinalis, Thlaspi arvense, Verbascum thapsus, etc. (Forcella and Harvey 1981). Eurasian taxa introduced for forage, etc., widely planted, and not considered weedy in most environments were not included in our weed categories (e.g., Dactylis glomerata, Phleum pratense, Poa pratensis, Medicago sativa, Trifolium pratense, T. repens. (B) The second weed category included native weed taxa that exhibit weedy behavior following disturbance, but are not prominent components of undisturbed vegetation (e.g., Chrysopsis villosa, Deschampsia elongata, Epilobium angustifolium, E. paniculatum, Grindelia squarrosa, and Rubus parviflorus).

Species nomenclature follows Hitchcock and Cronquist (1973), vegetation nomenclature is that of Pfister et al. (1977) and Mueggler and Stewart (1980).

In this report we use "infest" to indicate colonization in large numbers, a standard English dictionary definition, and restrict the term colonize to indicate few in number. Infestation was considered to be indicated when European weed coverage was actually 15% or was 10% of total plant cover.

RESULTS AND DISCUSSION

In the subalpine and mid-montane zones (i.e., *Abies lasiocarpa* and *Pseudotsuga menziesii* series of Pfister et al. 1977) alien weeds were



Relationships of 14 paired roadside/native vegetation plots along a transect Fig. 1. from Lolo Pass to Missoula, Montana. Data columns represent: (a) abbreviated habitat type designations (see below), (b) plot distance from Lolo Pass, (c) coverage of alien weeds in roadside plots, (d) coverage of native weeds in roadside plots, (e) coverage of trees in native vegetation plots, (f) coverage of native weeds in native vegetation plots, (g) coverage of alien weeds in native vegetation plots, (h) index of similarity by speciespresence between roadside and native vegetation plots, and (i) index of similarity by species-coverage between roadside and native vegetation plots. ABLA, Abies lasiocarpa; AGSP, Agropyron spicatum; ARUV, Arctostaphylos uva-ursi; CAGE, Carex geyeri; CARU, Calamagrostis rubescens; CLUN, Clintonia uniflora; FEID, Festuca idahoensis; FESC, F. scabrella; LIBO, Linnaea borealis; MEFE, Menziesia ferruginea; PIEN, Picea engelmannii; POSA, Poa sandbergii; PSME, Pseudotsuga menziesii; PHMA, Physocarpus malvaceus; THPL, Thuja plicata; TSHE, Tsuga heterophylla; VACA, Vaccinium caespitosum; VAGL, V. globulare; VASC, V. scoparium; XETE, Xerophyllum tenax: SYAL, Symphoricarpos alba.

almost entirely restricted to roadsides; they occasionally colonized, but never infested relatively undisturbed native vegetation (Fig. 1). The exchange of species that did occur between roadside and native vegetation was that of forest plants colonizing roadsides (e.g., *Alnus sinuata*, *Abies lasiocarpa*, *Picea engelmannii*, *Pinus contorta*, *Senecio* triangularis, Symphoricarpos alba, etc.).

In the low-montane zone (*Pinus ponderosa* series) and extending into the grasslands (*Festuca idahoensis*, *F. scabrella*, and *Agropyron spicatum* series of Mueggler and Stewart 1980), however, colonization and infestation of native vegetation by roadside Eurasian weeds increased markedly (Fig. 1f, g, h). Indices of similarity between roadsides and adjacent communities often exceeded 50% on a coverage basis (Fig. 1h). Coverage of alien weeds in low-montane and grassland vegetation ranged from about 20 to over 100% (Fig. 1f). Such coverage values suggest that introduced plants can greatly reduce the abundance of plants supplying economically important forage and forest products in low-montane and grassland areas of western Montana. It should be noted, however, that nearly all northern Rocky Mountain vegetation types that are not under intensive cultivation are grazed by livestock to some extent, with grassland and low-montane vegetation receiving more use than mid-montane and subalpine environments (Mueggler and Stewart 1980, Pfister et al. 1977). The results portrayed in Fig. 1 must partially, but not fully, reflect this pattern of land utilization.

In mid-montane forests, intensive disturbance (clearcut logging) enabled introduced weeds to colonize and infest, with absolute coverage up to 60% (Table 1c). Wildlife and livestock movements, forage production and tree regeneration might all be adversely affected by the abundance of alien weeds in these sites (cf. Anderson 1977, Chap. 1). The very lowest habitat types of the *Abies lasiocarpa* series was the upper limit of introduced weed colonization (Table 1). Species such as *Cirsium arvense* and *C. vulgare* were able to infest *A. lasiocarpa/ Linnaea borealis* habitats, but not cooler and wetter environments even though they were present along proximal logging roads. Native weedy species such as *Anaphalis margaritacea*, *Epilobium* spp. and *Rubus parviflorus* were prominent in these high elevation sites as well as in warmer and dryer forest sites at lower elevations (Table 1c, d). Perhaps native taxa competitively displace aliens in cool, moist environments.

Two factors that appear likely to control the ability of alien weeds to infest relatively undisturbed vegetation in our study are: (a) quantity of radiation incident upon the herbaceous vegetation layer, and (b) climate. Percent light reaching herbaceous layers of plant communities increases as arboreal canopy cover is reduced (Daubenmire 1968); light intensity is also an important factor in weed plant growth (Harper 1977). The natural reduction in tree coverage along a cool-moist to warm-dry vegetation gradient (Fig. 1, cf. Pfister et al. 1977) may be the prime factor allowing alien weed infestation of native vegetation (Frenkel 1970). Similarly, reduction in canopy cover by clearcutting facilitates weed colonization and infestation in formerly weed-free communities (Table 1, Fig. 1).

Climate may also limit weed infestations (Lindsay 1953, Salisbury 1961). To explore this possibility we pooled, by vegetation zone, all of our weed coverage data for 53 native and 71 roadside communities (from unpublished surveys), and then compared native and roadside coverage means to Weaver's (1979, 1980) climatic summarizations for each vegetation type (Table 2). (No statistical comparisons of weed and climatic data were made because of the inherent variability of

Habitat type		b	с	d	e	f	Stand age	Stand-county	
					(5.4				
Abla/Vasc-Vasc	0	0.0	0.0	32.1	67.6	4.1	6	1-Lincoln	
Abla/Mefe	0	0.0	0.0	57.5	97.5	1.0	6	4-Lincoln	
Abla/Mefe	0	0.0	0.0	6.5	59.1	6.1	6	1-Missoula	
Abla/Xete-Vagl	3	0.5	0.3	38.1	64.1	0.0	1	3-Lincoln	
Abla/Libo-Vasc	2	0.3	0.2	22.3	58.8	16.5	6	2-Lincoln	
Abla/Libo-Libo	8	29.3	19.8	39.9	67.6	0.6	2	1-Flathead	
Pien/Libo	7	8.7	5.2	38.9	60.1	0.0	1	2-Flathead	
Tshe/Clun	4	17.9	16.1	70.7	90.0	1.5	4	9-Lincoln	
Thpl/Clun-Clun	3	23.4	30.5	67.0	130.1	0.5	4	10-Lincoln	
Thpl/Clun-Clun	4	6.3	2.0	7.2	32.0	3.8	3	8-Lincoln	
Psme/Libo-Syal	7	30.8	27.5	32.6	88.7	3.2	3	1-Granite	
Psme/Cage	3	62.3	63.6	64.1	102.1	3.6	7	1-Mineral	
Psme/Caru-Caru	7	10.6	7.7	16.8	72.9	1.0	6	6-Lincoln	
Psme/Caru-Caru	5	21.5	16.2	32.8	75.2	1.5	4	7-Lincoln	
Psme/Caru-Aruv	3	1.8	1.5	9.8	83.1	1.7	6	5-Lincoln	
Psme/Caru-Aruv	5	15.8	7.5	11.2	47.4	1.1	5	5-Missoula	
Psme/Phma-Phma	5	39.5	42.5	44.0	107.7	6.1	5	6-Missoula	
Psme/Fesc	4	26.3	16.5	17.1	62.7	0.6	4	4-Mineral	

TABLE 1. CHARACTERISTICS OF CLEARCUT FORESTS BY HABITAT TYPES. (a) Number of Eurasian weed species, (b) coverage of Eurasian weeds as percent of total plant coverage, (c) actual percent coverage of Eurasian weeds, (d) total weed coverage, (e) total plant coverage, (f) tree-species coverage. Habitat types arranged along a presumed temperature-precipitation gradient.

both data sets.) The marked increase in alien weed coverage in native vegetation of *P. ponderosa* and grassland series is most closely linked to the number of months with one or fewer frosts; subalpine and midmontane forests have no months without frosts, whereas warmer and dryer environments have three months with one or no frosts. Length of drought is also associated with alien weed abundance in native vegetation (Table 2). Along roadsides and in clearcut forests, where introduced weed coverage is relatively high through all but the coolest and wettest vegetation types, mean July temperature (and perhaps duration of drought) is most closely associated with weed abundance (Table 2). Lindsay (1953) has previously shown that July temperature may play an important role in limiting Eurasian weed distributions and abundance in north-central North America.

There are a number of possible explanations for the lack of alien weeds in western Montana's subalpine zone, and their relative abundance on mid-montane slopes and lower environments. Seven explanations are listed below; they are not mutually exclusive, nor are any supported by conclusive evidence.

(1) Native weeds are better adapted to local subalpine environments than are alien weeds. Physiological limitations as well as competitive constraints may exclude aliens from high-montane sites.

(2) The majority of alien weeds in North America are of temperate

TABLE 2. COMPARISON OF CLIMATIC MEASUREMENTS IN SIX VEGETATION ZONES IN WESTERN MONTANA (from Weaver 1979, 1980) AND THE ABSOLUTE COVERAGE OF INTRODUCED WEEDS IN ROADSIDE AND NATIVE VEGETATION IN THOSE ZONES. Vegetation zones are ordered along a precipitation gradient from wet (left) to dry (right). Abla, Abies lasiocarpa; Psme, Pseudotsuga menziesii; Pipo, Pinus ponderosa; Fesc, Festuca scabrella; Agsp, Agropyron spicatum; and Bogr, Bouteloua gracilis/Stipa comata.

	Vegetation zone									
Measurement	Abla	Psme	Pipo	Fesc	Agsp	Bogr				
Mean July Temp. (°C)	14	17	20	17	20	21				
Mean Jan. Temp. (°C)	-8	-8	-3	-6	-7	-8				
Mean annual precipitation (cm)	82	58	55	43	38	35				
Number of months with 1 or fewer frosts	0	0	3	3	3	3				
Drought period (months)	0	0.3	1.7	2.0	1.8	2.0				
Percent coverage of introduced weeds in roadside vegetation. Mean ± standard deviation (sample size)	5.4 ±8.2 (8)	20.3 ± 16.0 (20)	43.9 ± 19.3 (13)	46.8 ± 24.4 (5)	30.8 ± 19.7 (9)	28.0 ± 23.2 (16)				
Percent coverage of introduced weeds in native vegetation. Mean ± standard deviation (sample size)	0.3 ± 0.5 (7)	0.5 ± 0.9 (14)	24.8 ± 25.5 (4)	62.8 ± 36.2 (4)	21.9 ± 19.2 (6)	3.3 ± 5.6 (18)				

or subtropical Eurasian origin. The relatively mild environments (i.e., long frost-free periods, high July temperatures; Table 2) to which they are restricted in western Montana may reflect the habitats whence they originated (Moore and Perry 1970, Mulligan 1965, Salisbury 1961). Unfortunately, weed plants originating in one climate are often much better adapted to quite different climates in foreign regions (Moore and Perry 1970, p. 73). Moreover, it is often difficult just to determine which country or region a specific weed is native to, let alone its exact native habitat (Mulligan 1965).

(3) Alien weeds that have the potential to infest subalpine zones are selected against and/or genetically changed during transcontinental migrations to the northern Rocky Mountains from their point(s) of introduction. Lindsay (1953) claimed *Hieracium aurantiacum* to be of a European alpine origin. Thus it might be expected to possess the ability to invade disturbed alpine and subalpine sites. However, this plant has migrated to the northern Rocky Mountain region (where it is currently spreading; Forcella and Harvey 1981), and neither here nor in the northeastern USA, where it is common, does the species infest subalpine environments. Rather, *H. aurantiacum* thrives in low-elevation roadsides and pastures where it is often considered noxious.

(4) Species richness is normally lower in subalpine environments than at lower elevations (Whittaker 1965). Therefore the pool of taxa

1983]

MADROÑO

that could behave as weeds is smaller in subalpine vegetation than elsewhere. The low number of potential weeds physiologically capable of infesting subalpine environments will reduce the probability of such weeds successfully migrating to foreign subalpine sites.

(5) Subalpine environments are analogous to small islands resting upon a vast sea of low elevation landscapes. The probability that alien weeds tolerant of subalpine conditions will reach such limited sites is low (cf. MacArthur and Wilson 1967).

(6) Many weeds may have evolved in response to land use by humans (Anderson 1952, Stebbins 1965). Throughout the world land use in the subalpine has been relatively minor in comparison to lower elevations (Espenshade and Morrison 1974). Thus not only is the landscape available for rapid weed colonization extremely limited in the subalpine zone but the selection pressure for weed behavior is reduced as well.

(7) Eurasian weeds may well occur in subalpine environments of the northern Rocky Mountains, but they are not recorded as alien taxa. The most conspicuous upper montane weed of the northern Rocky Mountains is *Epilobium angustifolium*, a circumboreal species. Despite differing polyploid levels, European and American material of *E. angustifolium* is extremely similar morphologically (Salisbury 1961). Possibly, Eurasian *Epilobium* was introduced into North America and subsequently proliferated without being recognized as Eurasian.

CONCLUSIONS

As a group, Eurasian weeds seem unable to tolerate the cool, moist conditions of subalpine environments, whether the site is shaded or light-saturated. In the mid-montane zone, temperature and moisture conditions seem adequate for introduced weed infestations, but the shade of arboreal canopies apparently preclude effective colonization by these species in undisturbed sites. The increase in light intensity within *Pinus ponderosa* vegetation allows significant Eurasian weed infestation, and this continues into light-saturated grassland communities. Decrease in alien weed coverage in very warm, dry grassland (*Bouteloua/Stipa* series; Table 2) is likely related to the general lack of plant coverage and harshness of this zone.

Because land management is becoming increasingly intense and sophisticated, the importance of predicting differential weed infestation of native and disturbed vegetation from existing and future roads (as well as other developments) will increase accordingly. This report suggests that in western Montana primary interest in regard to introduced-weed control be aimed at the *Pinus ponderosa* and grassland vegetation series for relatively undisturbed vegetation. For highly disturbed vegetation, weed control interests need to be concerned with all vegetation types except the *Abies lasiocarpa* series. 1983]

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